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Trophic interactions between copepods and microplankton: A question about the role of diatoms

Abstract—Relationships among microplankton composition, copepod diet, and egg production are examined with data from gut content analysis of copepods from California coastal waters and from the Irish Sea, feeding and egg production experiments on *Acartia tonsa* off southern California, and egg production measurements on copepods from a subtropical estuary (Port Everglades, Florida), temperate shelf waters (southern California, Irish Sea), and the open ocean (Gulf Stream). The copepod species studied appeared to feed preferentially on dinoflagellates and microzooplankton relative to diatoms. Patterns of variability in egg production conform, generally, to changes in dinoflagellate and microzooplankton biomass, but seem to be independent of changes in diatom biomass.

Diatoms historically have been associated with productive marine ecosystems and with food chains that lead, through copepods, to major fisheries (Riley 1947). As a result, diatom biomass has been considered an important component of the copepod diet. We argue here, however, that diatom biomass may compose only a small part of the copepod diet. Other kinds of microplankton, such as photosynthetic dinoflagellates and microzooplankton, may be responsible for providing a major portion of total nutrition of copepods, as well as much of the energy for their reproduction.

Our arguments are based on a compilation of results from our earlier research as well as from recent work. Three data sets are presented: diets of six copepod species determined by analysis of the gut contents of specimens from coastal ecosystems; results from bottle-incubation experiments in which the food, diet, and egg production of the nearshore copepod, *Acartia tonsa* were measured; and egg production rates and microplankton (=phytoplankton and microzooplankton) composition data from estuarine, coastal, and oceanic habitats.

The diets of six species of copepods from coastal southern California and Irish Sea waters were inferred from in situ measurements of the concentrations and composition of algal and animal pigments in the gut. Certain algal carotenoids are useful as taxonomic markers, permitting phytoplankton composition to be determined at approximately the class level. Carotenoids characteristic of animal biomass have also been identified (Cheeseman et al. 1967), and pigment content is roughly proportional to biomass (Liaaen-Jensen 1979). Pigments, extracted in 90% aqueous acetone from copepod gut contents and from microplankton filtered from water samples, were isolated and measured by reverse-phase liquid chromatography. The details of the techniques that were used have been published elsewhere (Kleppel and Pieper 1984; Kleppel et al. 1988).

The second data set consists of 10 bottle-incubation experiments performed to investigate the relationships among food, diet, and egg production of *A. tonsa* in the nearshore waters off Los Angeles. The experiments were performed between November 1986 and October 1987. Adult females (~12 liter^{-1}) were incubated in 2-liter polyethylene bottles for 24 h in the presence of particles from the collection site. Experiments were performed in triplicate with coincident, triplicate initial, and control (no copepods) samples. Microscopically enumerated phytoplankton and microzooplankton, preserved in Lugol's iodine solution, were measured with an ocular micrometer. Calculated cell volumes were converted to es-

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Table 1. Locations of copepod egg production experiments and the copepod species studied.

Area and date	Ecosystem	Location	Species
Port Everglades, Nov 89	Estuary	26°05.0'N, 80°06.0'W	*Acartia tonsa*
Irish Sea, May 89	Shallow sea	54°05.7'N, 4°55.0'W	*Temora longicornis* *Calanus helgolandicus*
		54°04.8'N, 4°49.5'W	*T. longicornis* *Centropages hamatus*
		54°07.2'N, 4°57.2'W	*C. helgolandicus* *Acartia clausi*
		54°06.7'N, 4°49.6'W	*T. longicornis* *C. hamatus* *A. clausi*
Gulf Stream, Sep–Oct 88	Oceanic	38°27.9'N, 70°48.8'W 37°31.3'N, 70°24.8'W	*Centropages furcatus* *C. furcatus*
Los Angeles, inshore, Nov 87–Oct 88	Coastal	33°45.4'N, 118°13.1'W	*A. tonsa*

timates of C biomass with the equations of Strathmann (1967) for phytoplankton and Beers and Stewart (1970) for microzooplankton. Recent studies suggest that the latter equations may underestimate the actual biomass (Putt and Stoecker 1989), but the relative rankings observed in the data should be unaffected. Ingestion rates were estimated with the equations of Frost (1972). Eggs were counted and measured, and their C contents were estimated from an empirically derived egg C : volume ratio (1.6×10^5 ng C mm^{-3} egg volume).

The third data set was compiled to examine the relationship between egg production and the food environment of copepods in a more general context. This data set encompasses egg production measurements on copepods (six species) from various ecosystems (Table 1). The kinds of systems studied were a subtropical estuary (Port Everglades, Florida), temperate waters on a continental shelf (off Los Angeles, California, and in the Irish Sea) and two stations in the open ocean (in the Gulf Stream). Microplankton samples were collected coincidentally with samples for egg production studies. Estimates of ambient dinoflagellate, microzooplankton, and diatom biomass were generated from pigment data or microscope counts from these samples.

Egg production experiments were performed by incubating individual female copepods in 50-ml plastic centrifuge tubes filled with 100-μm screened seawater for 24 h. Copepods and water (with microplankton) were from the upper 30 m of the water column at about the same location. Samples were preserved with Lugol's iodine and settled for 24 h before microscopic counting of eggs.

Because these experiments were conducted on species of varying size, egg production rates were expressed as mass of egg C (mass of female C)$^{-1}$ d^{-1}. It was not possible to measure the C content per egg in each experiment. Therefore, egg diameters were measured and egg C contents were estimated from an equation relating microzooplankton biomass, C, to volume, V. The equation was derived by regression with the data of Morey-Gaines (1980) along with our own measurements (Fig. 1). Adult female copepod biomasses were obtained from the literature.

Phytoplankton pigment concentrations were converted to biomass with C : carotenoid ratios. The ratios were typically derived from triplicate measurements of samples collected during each experiment. Phytoplankton C biomass estimates for these ratios were based on cell volume : C conversions (Strathmann 1967) performed on microscopically examined phytoplankton samples that were collected coincidentally with samples for pigment analysis. Microzooplankton biomass was estimated from body carotenoid content by the equation of Kleppel et al. (1988).

A pigment-ratio approach was used to ascertain whether the composition of the diet reflects the distribution of phytoplankton

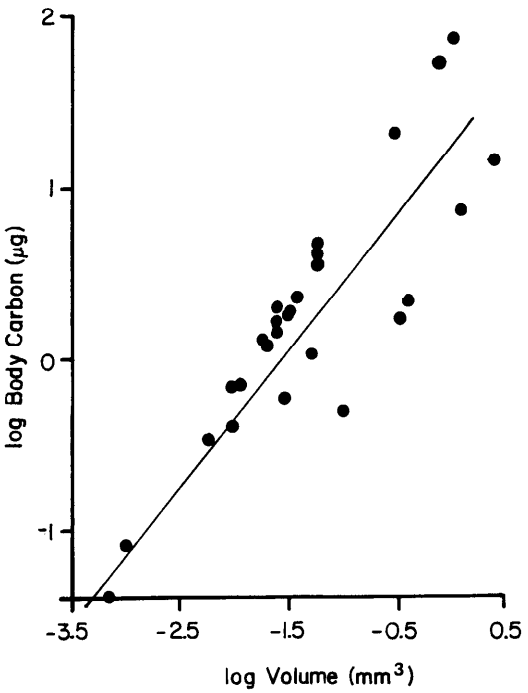

Fig. 1. Least-squares linear regression of microzooplankton C biomass, C, on body volume, V. Data were compiled from measurements by Morey-Gaines (1980) and by us. The data set includes, but is not limited to, information on copepod egg volume and C. The regression equation is log C = 0.75 log V − 1.21 (N = 27; r^2 = 0.75; $P < 0.001$).

taxa and microzooplankton in the environment. Ratios of dinoflagellate : diatom carotenoid concentrations (i.e. peridinin : fucoxanthin) and ratios of animal : diatom carotenoid concentrations (i.e. astaxanthin + canthaxanthin : fucoxanthin) were computed from pigments measured in copepod guts and in the ambient microplankton (the food environment of the copepod). Although fucoxanthin is a common golden-brown algal pigment, microscopic examination of representative samples indicated that diatoms were the principal sources of this pigment.

Pigment ratios are plotted for microplankton and for copepod samples from studies conducted off San Onofre and Santa Catalina Island, California, and in the Irish Sea (Fig. 2). Ratios of animal : diatom pigments are not presented for the San Onofre study (Fig. 2a) because the technique for estimating animal pigment content in the copepod gut had not been developed at that time. In the discussion which follows, we compare pigment ratios in the copepod guts to those in the ambient microplankton. The raw data for the studies off California have been presented elsewhere (Kleppel and Pieper 1984; Kleppel et al. 1988).

Pigment ratios in copepod guts were clearly different from those in the microplankton. Dinoflagellate : diatom, animal : diatom, or both pigment ratios were 1–2 orders of magnitude higher in the copepod guts than in the microplankton, suggesting a preference for dinoflagellates or microzooplankton or both relative to diatoms. Off Santa Catalina Island, peridinin : fucoxanthin ratios in copepods were lower than they were in the microplankton (Fig. 2d). At this time, primary production was low, and copepods fed predominantly on microzooplankton (Kleppel et al. 1988). The animal pigment : fucoxanthin ratio was, therefore, substantially higher in the copepods than in the microplankton.

Relationships between the food environment (ambient microplankton biomass), diet, and egg production by *A. tonsa* in the nearshore waters off Los Angeles were identified by correlation. Variability in egg production was poorly explained (r^2 = 0.01) by regression on ambient diatom biomass (Fig. 3a). Stronger correlations (r^2 = 0.39–0.40) were obtained between egg production and dinoflagellate (Fig. 3b) and ciliate (Fig. 3c) biomass. The strongest correlations (r^2 = 0.51) with ambient microplankton biomass, however, resulted from regressions of egg production on the sum of dinoflagellate + ciliate biomass (Fig. 3d).

Regressions between egg production and microplankton biomass in the diet (food eaten; Fig. 3e–h) were usually better than those between egg production and ambient microplankton biomass (food available; Fig. 3a–d). Although the correlation between egg production and diatom biomass remained weak (r^2 = 0.13; Fig. 3e), the regression of egg production on dinoflagellate + ciliate biomass in the diet explained 71% of the scatter in the relationship (Fig. 3h). The addition of diatom biomass to the data in Fig. 3h did not improve the relationship.

These results suggest that food compo-

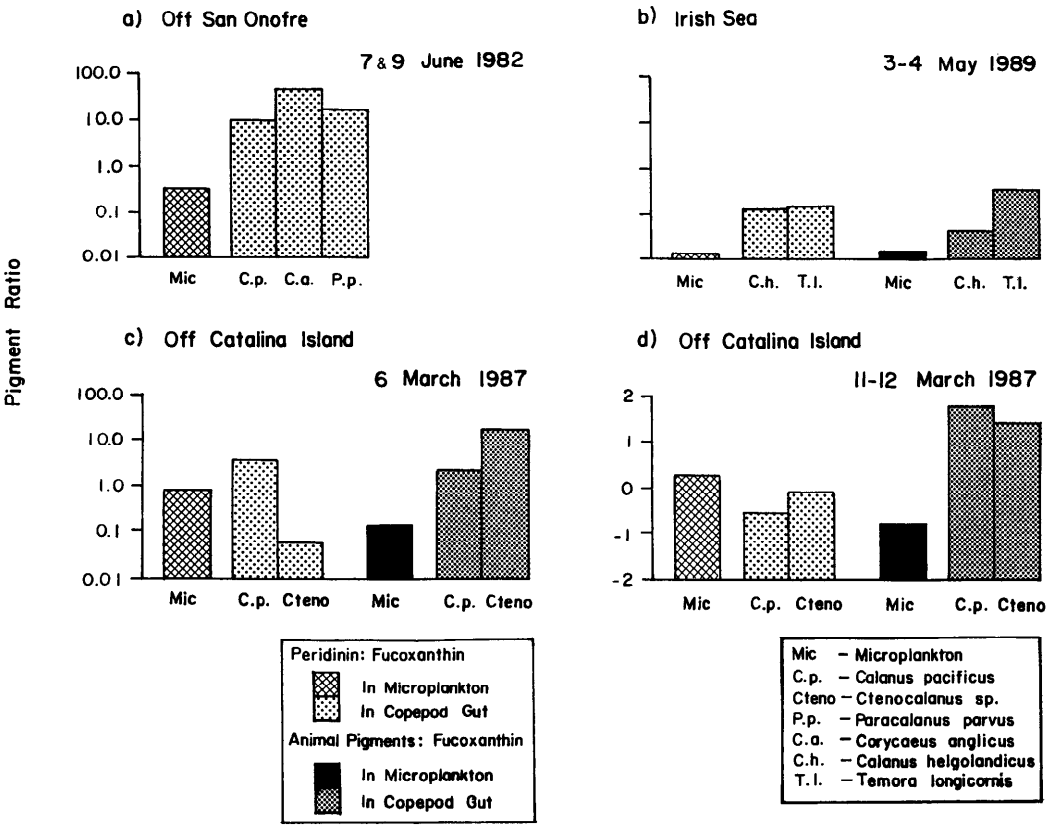

Fig. 2. Ratios of dinoflagellate : diatom carotenoid pigments (peridinin : fucoxanthin) and animal : diatom carotenoid pigments (astaxanthin + canthaxanthin : fucoxanthin) for microplankton and copepod gut content samples. a. Data were collected from three stations centered at 33°15′N, 117°35′W; the means are presented. b. Studies were centered at 54°06′N, 4°53′W. c. Data were collected at 33°30′N, 118°26′W. d. Data collected at four locations centered around 33°29′N, 118°23′W, which were sampled over 24 h while following a drogue; the means are presented.

sition influences the egg production rate of at least one copepod species. We therefore sought to determine whether our observations could be generalized beyond this study to a larger number of species and ecosystems. Data on egg production and microplankton composition were compiled from various experiments (*see Table 1*) to address this problem.

Experiments in the Irish Sea were performed during the North Atlantic spring bloom. Chain-forming centric diatoms of sizes (20–60 μm) thought to be readily ingested by copepods (Frost 1972; Bartram 1981) were abundant. Diatoms (20–50 μm) and ciliates (20–40 μm) were also abundant during the study in Port Everglades estuary. Gulf Stream samples were taken at the continental slope and Sargasso Sea boundaries, where diatoms were not abundant. Off Los Angeles, diatoms were frequently abundant, but they were usually small and did not contribute greatly to the microplankton biomass.

It was expected that substantial variability in the relationship between egg production and food would be introduced by differences among copepod species (and sizes), and by the physiological responses of the copepods to fluctuations in environmental factors other than food (e.g. temperature). The only effort to reduce the impacts of these sources of variability was to plot the data on log-log axes, which was also necessitated by the dynamic range of the data. In the patterns that emerged (Fig. 4), a general co-

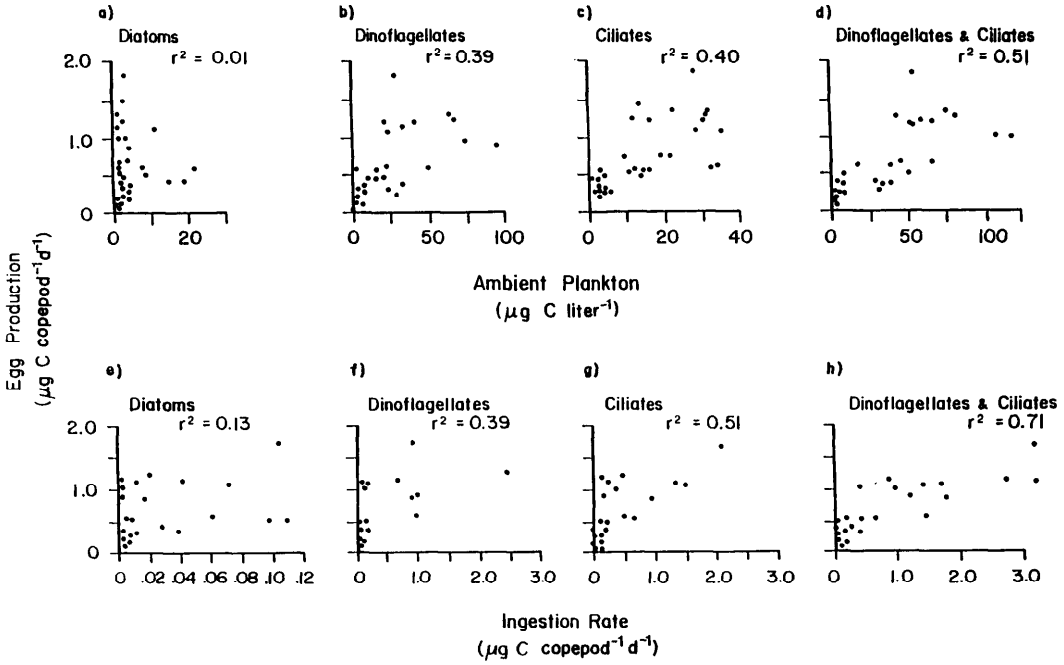

Fig. 3. Egg production of the copepod, *Acartia tonsa,* in nearshore waters off Los Angeles, California, plotted as a function of ambient concentrations (above) and dietary concentrations (below) of diatoms, dinoflagellates, ciliates, and dinoflagellates + ciliates. The r^2 values are from least-squares linear regression.

variance of copepod egg production was apparent with certain, but not all, components of the food environment. Egg production was correlated with dinoflagellate and microzooplankton biomass (Fig. 4a, b: r^2 = 0.76 and 0.53) but not with diatom biomass (Fig. 4c: r^2 = 0.0001). The data probably describe only a portion of the range of responses of copepod egg production to food availability. One would expect, for instance, that egg production would saturate at high food concentrations. A response threshold similar to that seen for microzooplankton biomass (Fig. 4b) might also have been observed for dinoflagellate biomass (Fig. 4a) had equally low dinoflagellate concentrations been present.

Considerable data exist to corroborate our findings. Evidence of the potential dietary importance of dinoflagellates and microzooplankton is accumulating (Porter et al. 1979; Stoecker and Sanders 1985; Gifford and Dagg 1988). Further, our observations are consistent with the results of laboratory studies (Morey-Gaines 1980; Stoecker and Egloff 1987) in which diets composed of certain dinoflagellates and ciliates have been found to enhance copepod egg production. It is noted, however, that some dinoflagellates appear to be poor foods (Huntley et al. 1986) and that not all microzooplankton are eaten (Stoecker and Egloff 1987).

Copepod egg production is thought to be limited by both the amount and quality of available food (Checkley 1980). Foraging copepods apparently can distinguish between the nutritional attributes of particles and, when it is efficient to do so, will feed on the more nutritious foods (Cowles et al. 1988). Dinoflagellates tend to be more nutritious than diatoms. Hitchcock (1982) determined the relationships between cell volume and protein, carbohydrate, and lipid content in diatoms and dinoflagellates grown in axenic cultures. Over a range of cell sizes typical of the particle sizes consumed by copepods (diam = 5.8–57.6 μm), dinoflagellates contain roughly 1.1–3.5 times more lipid and carbohydrate and 1.8–6 times more protein than diatoms contain. Ciliates also seem to be rich protein and lipid sources

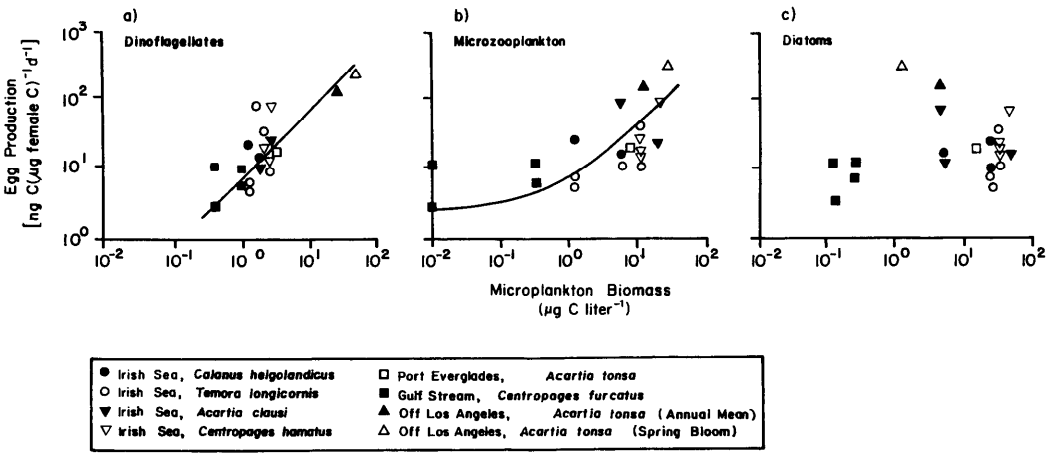

Fig. 4. Copepod egg production (EP) rate plotted as a function of the biomass (C) of dinoflagellates, microzooplankton, and diatoms. Data are compiled from results of studies in Port Everglades, Florida (subtropical estuary), off Los Angeles, California (temperate shelf), the Irish Sea (shallow, temperate sea), and the Gulf Stream (oceanic system). Regression equations: for dinoflagellates—log EP = 0.98 log C + 0.97 (r^2 = 0.76; N = 21; P < 0.001); for microzooplankton—EP = $0.73e^{0.12\,C}$ (r^2 = 0.53; N = 21; P < 0.05); for diatoms—log EP = 0.008 log C + 1.35 (r^2 = 0.0001; N = 21; P > 0.05).

relative to phytoplankton (Verity and Langdon 1984; Claustre et al. 1988).

Results from recent sedimentological and geochemical studies (Smetacek 1980) also indicate that, while diatoms may be important in the copepod diet, the link between diatom blooms and copepod grazing may be weaker than previously thought (Riley 1947). A model of the spring diatom bloom in the North Atlantic attributes the demise of the bloom to nutrient limitation; grazing by the dominant large copepod, *Calanus finmarchicus,* does not significantly affect its dynamics (Frost 1990). Keller and Riebessell (1989) reported that only 11% of the diatom C produced during a bloom in a Narragansett Bay mesocosm was lost to grazing. About 68% of the diatom C was lost to sedimentation and respiration. It would appear in this case that the diatoms were not a major food source.

It should be emphasized that copepods do eat diatoms; we do not suggest that diatoms are avoided. When other kinds of foods are scarce, diatoms may be critical in sustaining copepod populations. Further, the lack of size-frequency information in our gut pigment data may create a bias. Small diatoms, which may be unavailable to copepods, contribute to the ambient fucoxanthin concentration but not to that in the gut. Our microscopic analyses off Los Angeles, however, and the pigment data from the Irish Sea, which were collected when large diatoms were abundant, lead us to suspect otherwise. Evidence is accumulating to suggest that diatom biomass may be less significant in the diets of many copepod species than was previously thought. Simultaneously, the abundance in the sea of organisms such as aloricate ciliates is now more fully appreciated due to improved preservation and counting techniques. In this context, the role of diatoms in the important food chains to which they have generally been assigned might be worth reconsidering.

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